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Comparison of performance on memory-guided saccade and delayed spatial match-to-sample tasks in monkeys

Ioan Opris ^{*}, Andrei Barborica, Vincent P. Ferrera

Department of Psychiatry, Center for Neurobiology and Behavior, Columbia University, New York, NY 10032, USA

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Abstract

To investigate the sources of spatial error in memory-guided saccades (MGS), we have trained monkeys on two different tasks: a MGS task and a delayed spatial match-to-sample (MTS) task. We first tested the effect of introducing a post-saccadic visual feedback on the accuracy of MGS. We found that visual feedback had a pronounced effect on the systematic saccade error, but less of an effect on the variable error. Visual feedback can improve the accuracy of saccadic eye movements over several days, while feedback removal can decrease accuracy in a reversible way. These effects also depend both on target eccentricity and the duration of the memory delay. To test whether saccade error is due to the accuracy of spatial memory storage or arises downstream from that memory, we measured behavioral performance on a spatial MTS task both before and after training with visual feedback. The results showed no significant difference in performance of the MTS task before and after feedback training despite significant changes in MGS accuracy. The results suggest that the accuracy of spatial memory is not the source of the systematic errors that accompany MGS.

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Keywords: Monkey; Saccade; Feedback; Systematic error; Variable error; Spatial working memory

1. Introduction

Several studies in monkeys have demonstrated that saccades made to the remembered location of visual targets (memory-guided saccades, MGS) have larger systematic errors compared to visually guided saccades (VGS) (Gnadt, Bracewell, & Andersen, 1991; Stanford & Sparks, 1994; White, Sparks, & Stanford, 1993). MGS are slower and less accurate than VGS, with the errors accumulating during the first few hundred ms of the delay (Gnadt et al., 1991). The saccade inaccuracy found in memory tasks seems to be different from those caused by lesions or chemical inactivation in prefrontal or parietal cortex (Dias & Segraves, 1999; Funahashi, Bruce, & Goldman-Rakic, 1993; Li, Mazzoni, & Andersen, 1999). The exact nature of such saccadic errors, and whether they arise from the encoding, storage, or motor

stages of the sensorimotor transformation, is a matter of debate. One hypothesis is that the errors are introduced during translation from a perceptual memory of the cue location to a memory of the intended eye movement (Gnadt et al., 1991). Another view suggests that saccade inaccuracies are introduced in the motor output downstream from the superior colliculus (Stanford & Sparks, 1994). Current evidence favors the motor hypothesis.

Saccade inaccuracy in monkeys has been expressed in terms of ‘systematic’ and ‘variable’ errors (White et al., 1993). The ‘systematic error’ is defined as the difference between target position and eye position at the end of the first saccade initiated after the go signal, while the ‘variable errors’ are defined as the spread of saccade endpoints about their mean (Stanford & Sparks, 1994; White et al., 1993).

To address the source of saccade inaccuracy, we manipulated the accuracy of MGS by providing or withholding post-saccadic visual feedback. Visual feedback was provided after the execution of the saccade and before the reward was given. Visual feedback improves the accuracy of MGS over several days, while feedback removal decreases saccade accuracy (Opris,

^{*}Corresponding author. Address: Department of Neurobiology, School of Medicine, Yale University, 333 Cedar Street, SHM C303, New Haven, CT 06510, USA. Tel.: +1-203-785-5724; fax: +1-203-785-5263.

E-mail address: ioan.opris@yale.edu (I. Opris).

Barborica, & Ferrera, 2000). Here we investigated the effect of feedback on systematic and variable saccade errors while varying saccade direction, saccade amplitude, and delay interval duration.

We used a second task, delayed spatial match-to-sample (MTS) to independently test the accuracy of spatial working memory. The MTS task was very similar to the MGS task in terms of encoding and storage of target location, but differed with respect to the manner in which that memory was used to generate the behavioral output. Changes in MGS performance before and after feedback training did not carry over to performance on the delayed spatial MTS task. These results further support the notion that the inaccuracy seen in MGS arises downstream from the storage of remembered target location.

2. Methods

Experiments were performed on two male rhesus monkeys (*Macaca mulatta*) weighing between 8 and 9 kg. All methods were approved by the Institutional Animal Care and Use Committee at Columbia University and the New York State Psychiatric Institute. Monkeys were prepared for experiments by surgical implantation of a post used for head restraint. Eye position was recorded using a monocular scleral search coil (Judge, Richmond, & Chu, 1980; Robinson, 1963). The system was calibrated by adjusting the gain, offset and phase of the eye position signal while the monkeys looked at targets of 5 or 10 deg eccentricity along the vertical and horizontal meridia. Monkeys were trained to sit in a primate chair for the duration of the experiment with their heads restrained and perform a visual fixation task. Correct performance of the task was reinforced by liquid reward.

2.1. Visual stimulation

Fixation targets were generated and controlled by a Cambridge Research Systems VSG2/3F video frame buffer with an on-board digital signal processor (Texas Instruments TMS 34020). The output from the video board was displayed on a calibrated 27 in. color monitor (Mitsubishi) with a 60 Hz non-interlaced refresh rate. The monitor stood at a viewing distance of 30 in. so that the display area subtended roughly 40 deg horizontally by 30 deg vertically. The spatial resolution of the display was 1280 pixels by 1024 lines. Fixation targets were small (0.5 deg) white squares presented on a uniform black background. The luminance of the fixation target was 65.0 cd/m², while the background was close to 0 cd/m² (below the photometer threshold). The frame buffer was programmed to send out digital pulses (frame sync) for timing purposes at the beginning of each video frame

in which a target was turned on or off. These pulses were recorded by the computer using a hardware timer (Lisberger Technologies), and stored together with the eye movement data. The experiments were performed on dim ambient light.

2.2. Behavioral tasks

VGS task. At the beginning of each trial, the monkey fixated a small white square (1.0 deg, 15 cd/m²). A small peripheral cue was flashed for 500 ms and the monkey was required to make a VGS landing within ± 2.0 deg of the cue location within 350 ms. Saccade eccentricities were 5, 10 and 14 deg and the cue locations were equally spaced (45 deg) around the clock. Target positions were randomly varied during each session.

Memory-guided-saccade-task (MGS and MFB). In this experiment we have used two versions of the MGS task. The first followed closely the original task developed by Goldman-Rakic and colleagues (Funahashi, Bruce, & Goldman-Rakic, 1989; Funahashi et al., 1993), called *memory-guided saccade* and shown in Fig. 1A. Also shown in Fig. 1A is the *memory-guided saccade with feedback (MFB)* task, which provided visual feedback after the saccade had been initiated but before reward delivery. In both tasks, at the beginning of the trial the monkey fixated a small white square (1.0 deg and 15 cd/m² in luminance) in the center of the display. While he fixated, a small (0.5 deg) white peripheral cue was flashed for 300 ms. The monkey was required to maintain fixation throughout the cue period and also throughout the subsequent delay period. At the end of the delay interval (500 or 1000 ms, randomly interleaved) the fixation target was extinguished and the monkey was allowed to make a saccade to the remembered location of the cue. The monkey was rewarded if his eye position was within a ± 5.0 deg square window around the peripheral cue location within 600 ms of fixation target offset. There were eight possible cue locations, equally spaced (45 deg) around the clock face at eccentricities of 5, 10, or 14 deg. Cue direction, eccentricity, and delay duration and were randomly selected for each trial. In the memory with feedback task, we added a visual feedback before reward delivery by presenting the cue for 200 ms at its original location. There was a delay of 500 ms between fixation target offset and feedback onset. As the saccade grace period (600 ms) was longer than the feedback delay (500 ms), it was technically possible for the monkeys to initiate the saccade after the feedback and still obtain a reward. However, we found only one trial with saccade latency greater than 500 ms and this trial was excluded from the analysis.

Spatial delayed MTS task. In the MTS task monkey fixated a central target while a peripheral cue (sample) was presented for 300 ms (Fig. 1B). After the cue was

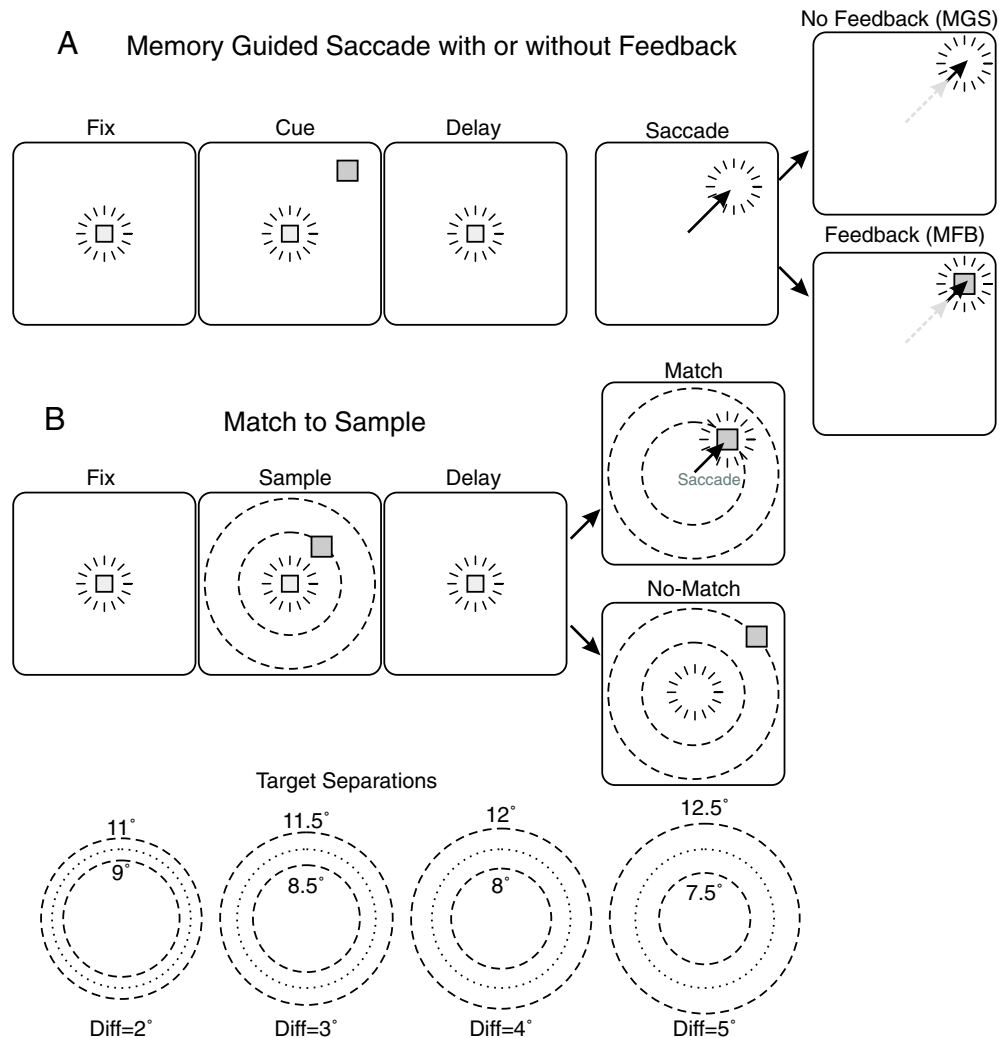


Fig. 1. Schematic representation of the behavioral tasks. (A) MGS task with or without feedback. Each square panel is an iconic representation of the visual display at different times during the task. The light grey square in the center of the display indicates the fixation point. The dark gray square represents the cue. The spoked ring indicates where the monkey is required to look. Arrows indicate saccades. (B) Delayed spatial MTS. Same conventions as A. The dotted circles indicate cue and target eccentricities. Arrows, spoked rings, and dotted circles are solely for the reader's benefit and were not displayed on the video monitor that the monkeys viewed.

extinguished, there was a delay of 1500 ms, and then a second peripheral target was presented either at the same location as the cue or at a different location. The central fixation target remained on during the presentation of the peripheral target on all trials. The cue and target differed only in eccentricity, not direction. The monkey was rewarded for making a saccade if the cue and target locations were identical (match = GO) and for withholding a saccade if they were different (non-match = NOGO). On match trials, eye position was required to be within ± 2.0 deg of the peripheral target within 400 ms of its appearance. On non-match trials, eye position was required to remain within ± 2.0 deg of the fixation target. Match and non-match trials occurred with equal probability. Non-match target locations were 2, 3, 4, or 5 deg distance from the cue location. The mean cue eccentricity was 10 deg. In comparing the

MTS and MGS tasks (either with or without feedback), it should be noted that the cue/sample and delay components of all tasks are identical. We assume that the encoding and storage of cue location is similar for all tasks and that only the manner in which the memory is translated into movement differs between MGS and MTS.

2.3. Data collection

The experiments were performed in two parts. In each experiment we ran two monkeys on memory-guided saccades with (MGS) and without feedback (MFB). In the first experiment, monkey A was first tested with feedback for 31 consecutive days (1 session per day), and then tested for 32 days consecutively without feedback. In the 31st day of the experiment, before switching to

MGS, we tested behavior on VGS task, for comparison. Before testing, monkey B received several days of training without feedback during which no data were recorded. Monkey B was then tested on MGS task for 24 consecutive days, and then switched to the MFB task for 32 consecutive days. In the 32nd day we tested behavior on VGS task, as well. For both MGS and MFB tasks we collected a minimum of 10 blocks (480 trials) each day. In the second experiment, we followed the same order, i.e. we ran monkey A first on MGS task and tested on MTS, then switched to MFB task, and tested on MTS. For monkey B we did the same but in a reversed order, i.e. we started with MFB and ended with MGS. For MGS and MFB we collected 50 trials per condition (50 trials \times 8 directions \times 1 delay) for a total of 800 trials per monkey, and for MTS task we collected twice 20 trials per condition (8 directions \times 8 eccentricities \times 1 delay \times 2 go/no-go conditions) for a total of 5120 trials per monkey.

2.4. Eye movement recording and analysis

Eye position was monitored using a monocular scleral search coil system (CNC Engineering). Separate horizontal (H) and vertical (V) eye position signals were fed through an analog differentiator (low pass, -3 dB at 25 Hz) to yield horizontal (H') and vertical (V') eye velocity. The eye position and eye velocity signals were then digitally sampled by computer at 1 kHz/channel and stored on disk for offline analysis. Eye position and velocity records were used to estimate saccade latency and amplitude. Polar eye velocity (R') was constructed from horizontal and vertical eye velocities using the formula:

$$R' = \sqrt{(H')^2 + (V')^2} \quad (1)$$

Then, polar eye velocity was digitally differentiated to yield polar eye acceleration (R''). Saccade onset was computed using an acceleration criterion ($R'' \geq 500$ deg/s²). Saccade offset was found using the complementary criterion ($R'' \leq 500$ deg/s²). This criterion was not always appropriate for small saccades, hence each trial was also checked by visual inspection.

In the MGS tasks, the saccade error was defined as the distance in degrees between the target location and the saccade endpoint. The saccades error time course has been fitted with an exponential function:

$$\text{err}(t) = a + b \exp(-t/\tau) \quad (2)$$

where t is the time in days, τ is the time constant, a and b are fitting parameters. The parameter b is positive when the error is decreasing with time and negative for increasing error.

In the MTS tasks we calculated the percentage of correct trials at each separation between match and

sample targets (2–5 deg) and plotted as a function of the separation in degrees. The points were fitted with a sigmoidal psychometric function (Eq. (3)). Threshold was taken as the separation at which performance reached 81% correct.

$$p(s) = 50 \times [1 + \tanh(s - \theta)] \quad (3)$$

where $p(s)$ is the percentage of correct trials as a function of the separation s in degrees, and θ is the separation threshold in degrees.

3. Results

We recorded the oculomotor performance of two monkeys (A and B) trained on MGS with and without visual feedback for 63 (monkey A) and 56 (monkey B) consecutive days. The saccadic eye movements performed in the presence of post-saccadic visual feedback have two steps. In the first step, the monkey performs the MGS with a certain amount of error and in the second step the animal makes the corrective saccade to the right location. Over time, the visual feedback helps the monkey to perform the first saccade more accurately. The absence of post-saccadic feedback results in gradually worsening saccade performance. To compare memory performance before and after feedback training we used a MTS task.

3.1. Comparison of monkey performance on MGS and VGS tasks

Saccades made in a MGS task are less accurate and slower than those made during a VGS task. Saccade errors usually contains an upward bias (upward hypermetric and downward hypometric saccades, Gnadt et al., 1991; White et al., 1993) and a memory dependent fluctuation (variable error) in saccade endpoints. In Fig. 2 we show the spread pattern of the endpoint of saccades performed during MGS vs. VGS tasks for both our monkeys. We note, however, that there are some differences among our monkeys: monkey A shows a shrinking pattern in the saccade amplitude for all directions, while monkey B displays the classical pattern of upward bias in the saccade endpoints. This effect appears to be larger as the eccentricity of the target increases.

3.2. The effect of visual feedback on the time course of saccade systematic error

Systematic errors were defined for each trial as the difference between target position and eye position at the end of the first saccade initiated after the go signal. The direction and amplitude of systematic error varied as a function of target direction and eccentricity, as

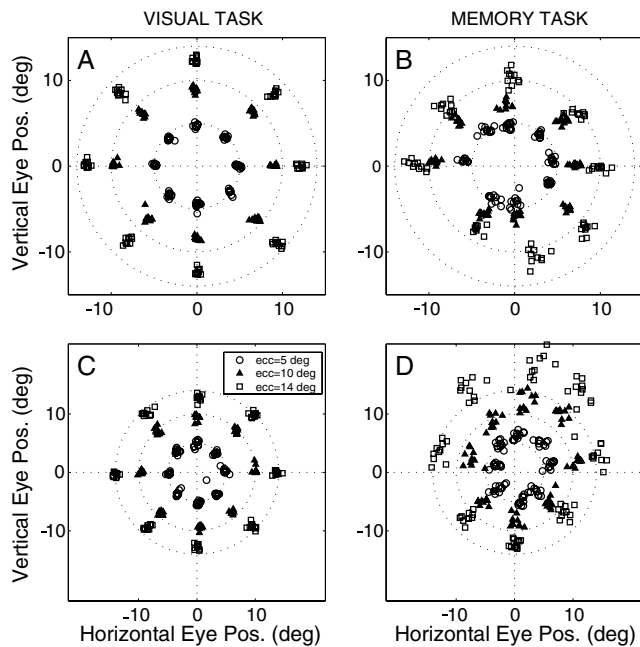


Fig. 2. The endpoint of saccades performed in the VGS task were displayed on the left column and the performance in the MGS task on the right column. The top row shows data for monkey A, and the bottom row for monkey B (note different scales). The tasks were run for both monkeys at three different eccentricities (5, 10 and 14 deg) and eight directions separated by 45 deg.

shown in Fig. 2B and D. To show the change in systematic error over time, we averaged the data over target direction in Fig. 3, which shows the time course of saccade error sorted by monkey, delay duration and target eccentricity. Visual feedback provided after the completion of the MGS task improved the accuracy of saccadic eye movements over several days. For monkey A (Fig. 3A and B), in the absence of feedback (MGS condition), the systematic error accumulated until it started to reach a plateau. Then, after 32 days, we added visual feedback (MFB condition), and monkey A improved his saccade accuracy on a time scale of a few days. Comparing MGS performance before and after feedback training, there was a statistically significant difference in the mean saccade error (t -test, $p < 0.00001$).

The effect of cue direction, cue eccentricity, delay duration, and session on systematic error was tested using a four-way ANOVA. As seen in Table 1, all four factors were highly significant ($p < 0.01$). Both the accuracy improvement and error accumulation were faster for larger eccentricities than for smaller ones. Comparisons were made by performing t -tests for all three pairwise combinations of the three eccentricities. Observations were paired by monkey, delay, target direction, and session. For both monkeys, all three comparisons were highly significant ($p < 0.0001$). The

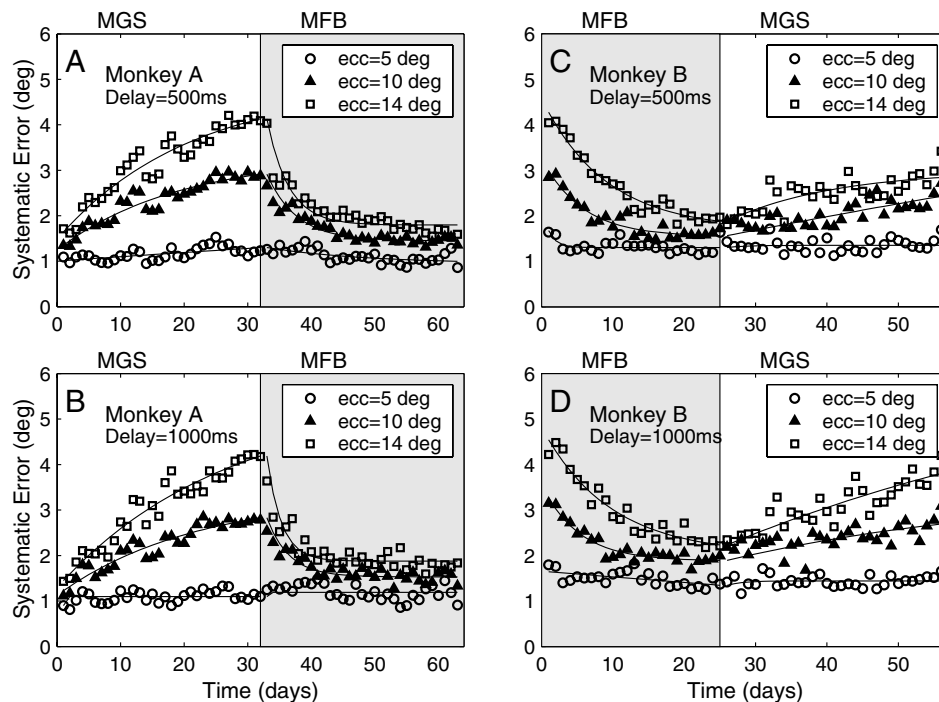


Fig. 3. Accumulation/improvement of systematic error. Performance in the memory-guided saccade without feedback task (MGS) is shown with a white background, while the performance on the MFB task is shown with a grey background. The average error is plotted as a function of time (days). The data are sorted by monkey, delay duration and target eccentricity.

Table 1
Results of a four-way ANOVA statistical analysis of the systematic and variable saccade errors for each monkey and task, with the session, direction, eccentricity and delay as factors

Error	Monkey	Task	Session			Direction			Eccentricity			Delay		
			<i>F</i>	<i>df</i>	<i>p</i>	<i>F</i>	<i>df</i>	<i>p</i>	<i>F</i>	<i>df</i>	<i>p</i>	<i>F</i>	<i>df</i>	<i>p</i>
SYS	A	MGS	105.39	28	0	697.69	7	0	5938.82	2	0	38.35	1	<10 ^{−9}
		MFB	111.83	33	0	215.65	7	0	1748.90	2	0	7.29	1	<0.0069
	B	MGS	33.84	33	0	91.40	7	0	2012.24	2	0	320.39	1	0
		MFB	47.00	21	0	97.04	7	0	1045.26	2	0	190.50	1	0
VAR	A	MGS	4.99	28	<10 ^{−15}	54.02	7	0	1124.53	2	0	146.57	1	0
		MFB	9.13	33	0	54.14	7	0	638.24	2	0	137.08	1	0
	B	MGS	13.71	33	0	144.43	7	0	1070.37	2	0	269.20	1	0
		MFB	4.28	21	<10 ^{−9}	88.21	7	0	561.78	2	0	163.64	1	0

Null probabilities stand for *p* values less than the smallest floating-point number that could be represented in Matlab.

differences between systematic errors for 500 and 1000 ms delay were also significant (paired *t*-test, $p < 0.0001$ for both monkeys). However, the magnitude of the eccentricity effect was much greater than the effect of delay duration (Fig. 4).

To characterize temporal changes an exponential fit was performed using Eq. (2). The average time constant for improvement with visual feedback was 5.4 days (± 2.8 s.e.), compared to 30.2 days (± 18.0 s.e.) for the deterioration in the absence of feedback. The time constants were also different across monkeys and eccentricities, with monkey *A* being faster than *B* and large eccentricities faster than small eccentricities.

To show that visual feedback changed the magnitude of systematic errors in a reversible fashion, the order of testing differed between the two monkeys. Monkey *A*

(Fig. 3A and B), was first tested on the MGS task until memory error reached plateau (32 days) and then switched to the feedback task (MFB). For monkey *B* (Fig. 3C and D) we reversed the order of the memory tasks. For both monkeys, systematic error increases during the MGS task, while during the MFB task the error decreases.

3.3. The effect of visual feedback on the time course of variable errors

In addition to systematic errors, we were also interested in the variable errors of saccades. Variable error is defined as the spread of saccade endpoints about their mean. The change in variable errors over time may indicate that there is a memory component carried by the

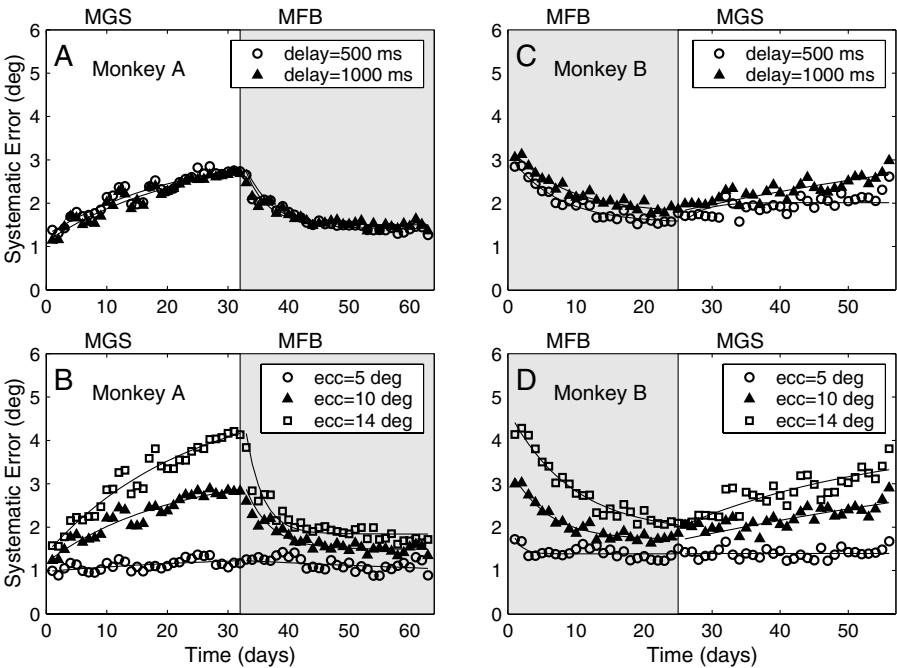


Fig. 4. Time course of saccade systematic errors for the MGS with and without feedback in two monkeys. (A, C) Saccade systematic error for different delays averaged over eccentricity; (B, D) Saccade systematic error for different eccentricities, averaged over delay duration.

saccade errors. To determine such an involvement, we have plotted in Fig. 5 the time course of the standard deviation of the saccade landing positions over time. We compared the feedback effect for different delays and eccentricities averaged over all directions. Note that the variable error for monkey B is typically twice as large as monkey A (note different scales for left and right columns in Fig. 5). At a glance, no consistent change in saccade spread over time is observed.

The effects of cue direction, cue eccentricity, delay duration and session on variable error were tested using a four-way ANOVA (Table 1). All four factors had a highly significant effect on variable error ($p < 0.01$) for each monkey and for each task condition (with or without feedback). Paired t -tests were performed to compare the variable errors for MGS and MFB tasks. The data were sorted by cue direction, cue eccentricity and delay duration (a total of 48 conditions: 8 directions, 3 eccentricities, 2 delays). The resulting p -value was less than 0.01 for 28/48 of the conditions in monkey A and 19/48 of the conditions in monkey B. Hence, the differences in variable error between the with-feedback and without-feedback conditions were not consistent. We conclude that there is no significant change in the mean of the variable errors with the task.

The magnitude of adaptive changes in saccade amplitude is known to depend on the timing of the appearance of the post-saccadic target relative to the saccade (Albano, 1996; Bahcall & Kowler, 1999, 2000; Shafer, Noto, & Fuchs, 2000), and the same may be true for the improvement seen in saccade accuracy with

feedback training. We measured the delay between saccade onset and visual feedback onset on each MFB trial to determine if it was in the range known to be effective for saccade adaptation. Averaged over all trials, the mean feedback delay for monkey A was 301 ms (± 11 ms s.d.), and for monkey B was 242 ms (± 13 ms s.d.). The trial-by-trial feedback delays were analyzed for each session using a two-way ANOVA with factors: cue direction and cue eccentricity. The results of the ANOVA fluctuated from session to session. The effect of cue direction was significant ($p < 0.05$) in 21/34 sessions for monkey A and 20/22 sessions for monkey B. The effect of cue eccentricity was significant in 19/34 sessions for monkey A and 12/22 sessions for monkey B. The mean feedback delay was computed each cue direction and eccentricity, as well as each session. The largest differences in mean feedback delay were 59 ms (monkey A) and 78 ms (monkey B). Hence all conditions had similar feedback delays of about 250–300 ms. Delays in this range are adequate, although not optimal, for inducing saccade adaptation in monkeys (Shafer et al., 2000).

3.4. Overall performance on MGS tasks

To determine if saccade errors were correlated with overall performance, we computed the percent of correctly completed trials for each session of MGS with and without feedback. Incorrect trials included those that were aborted due to fixation break during the cue or delay intervals and those where the saccade landed outside the fixation window. We did not distinguish

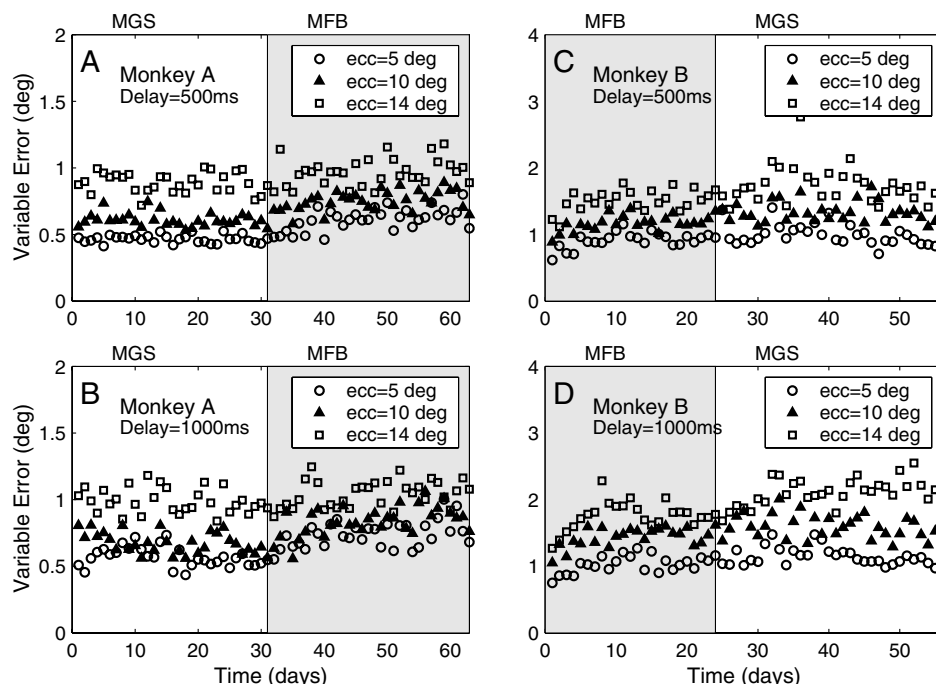


Fig. 5. Variable saccade errors. Same format as Fig. 3. Note different y-axis scales for the two monkeys.

between these two classes of error. A large proportion of incorrect trials might indicate that the fixation window was too small to accommodate the saccade error. As saccade error changed over time due to the introduction or removal of feedback, we split each block of MGS or MFB session in half and compared performance across the two halves. For monkey A, the average performance on memory-guided saccades without feedback (MGS) was 82.4% correct ($\pm 10.9\%$ s.d.) for the first 15 days, and 77.3% ($\pm 7.0\%$ s.d.) for the last 14 days. The difference was not statistically significant ($p = 0.15$, unpaired t -test). After feedback was introduced, the

performance for monkey A was 97.0% correct ($\pm 1.5\%$ s.d.) for the first 16 days, and 97.1% ($\pm 4.7\%$ s.d.) for the last 16 days ($p = 0.96$). For monkey B, without feedback, performance averaged 91.2% ($\pm 2.7\%$ s.d.) for the first 16 days, and 89.3% ($\pm 8.4\%$ s.d.) for the last 16 days ($p = 0.39$). With feedback, this monkeys performance was 89.9% ($\pm 1.5\%$ s.d.) for the first 12 days, and 94.2% ($\pm 2.4\%$ s.d.) for the last 11 days ($p < 0.0001$). Feedback appears to improve percent correct, whereas removal of feedback degrades performance, but these effects are small and do not suggest that the increasing magnitude of saccade error resulted in a large proportion of

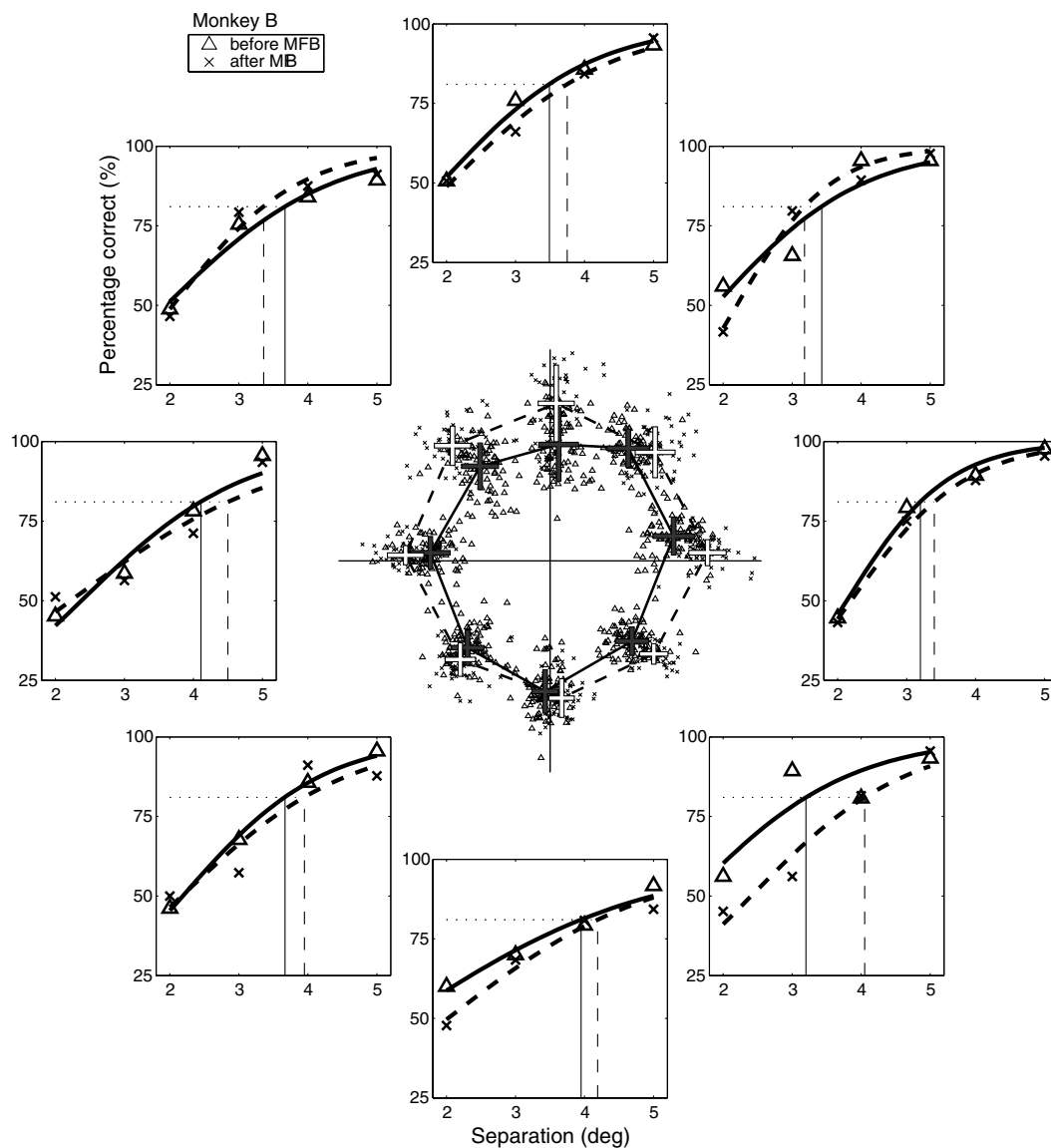


Fig. 6. MTS and MGS performance in monkey B. Performance (percentage of correct trials) in the MTS task before training (triangles/solid line) and after feedback training (x's/dashed line) with post-saccadic visual feedback plotted against the target separation in degrees. The data were fitted with a sigmoidal psychometric function (solid/dashed lines). The vertical lines represent the separation thresholds for 81% correct performance (solid—before, dashed—after). The polar plot in the center shows the saccade endpoints and their standard deviations before (triangles/gray filled crosses) and after (x's/white filled crosses) feedback training.

excluded trials. Overall, the percentage of trials excluded due to both fixation breaks and errant saccades was 11% and 9% for monkeys A and B, respectively.

3.5. Comparison of performance accuracy on MTS and MGS tasks

To measure memory accuracy we used a spatial MTS task having the matching and sample targets separated by 2–5 deg. We tested both monkeys on a MTS task before and after 3–4 weeks of training on the MGS task. The animal was rewarded if he made a saccade when the

cue and target locations matched and withheld a saccade otherwise. In Fig. 6, the outer ring of panels shows MTS performance as a function of target separation for each direction before (triangles) and after (x 's) feedback training for one monkey. The inner plot shows the saccade vectors before and after feedback training (delay = 1500 ms, ecc = 10 deg, matching the values in the MTS task). If there was a systematic improvement in MTS performance, the x 's for the MTS task (outer ring) should lie above the triangles and the “after” thresholds (dotted vertical lines) should lie to the left of the “before” thresholds (solid lines). In fact, there appears to be little systematic change in MTS performance. Fig. 7 shows the change in performance (difference in percent correct after–before, so positive change=improvement). Data are plotted for both monkeys as a function of separation. Each individual data point represents a different target direction. There was a significant improvement (t -test before vs. after, $p < 0.05$) in performance in only one case out of eight.

MTS thresholds were calculated by fitting Eq. (3) to the data. Fig. 8 compares thresholds to systematic and variable errors. In the top row, there is a significant decrease in systematic error after feedback training, but no significant change in MTS thresholds. In the bottom row, there is no significant change in either variable error or MTS threshold nor is there a significant correlation between the two. Although monkey B generally had larger variable errors than monkey A, their MTS thresholds were nearly identical.

4. Discussion

Our experiments reveal new insights into the systematic and variable errors of the saccadic eye movements during MGS task and how they depend upon the presence of a post-saccadic visual cue introduced after saccade execution. The results show that the post-saccadic feedback improved the accuracy of saccadic eye movements over several days depending on the target eccentricity of the saccade and the duration of the memory delay. This is in agreement with behavioral studies that have reported saccade inaccuracy (Gnadt et al., 1991; Stanford & Sparks, 1994; White et al., 1993) and saccade adaptation (Bahcall & Kowler, 2000) in humans and (Shafer et al., 2000) in monkeys. On the other hand, the discrimination performance in the MTS task and the variable errors in the MGS/MFB task, show very little dependence upon visual feedback.

An important finding in the present work, is that visual feedback provided after the completion of the MGS task, improved the accuracy of saccadic eye movements. In MGS tasks monkey performance shows a ‘default’ systematic error in saccade endpoints (Funahashi et al., 1989; Gnadt et al., 1991; Stanford & Sparks,

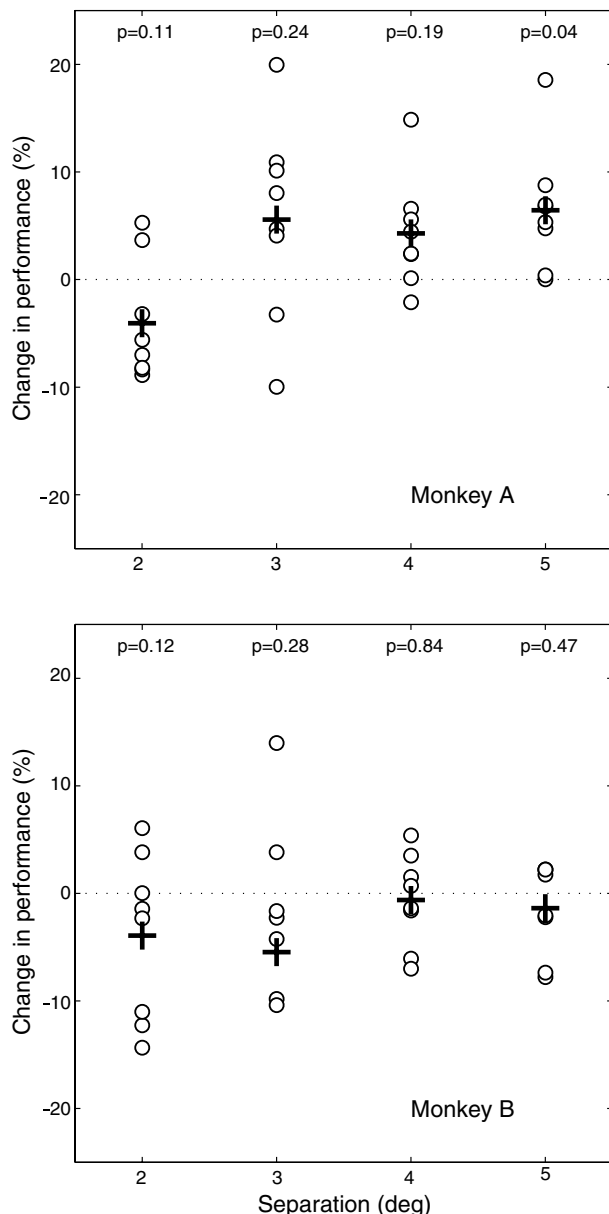


Fig. 7. Change in performance on MTS task. Open circles are percent correct for each direction and separation. Mean performance for each separation averaged over direction plotted as +'. p -values are results of unpaired t -tests (before vs. after).

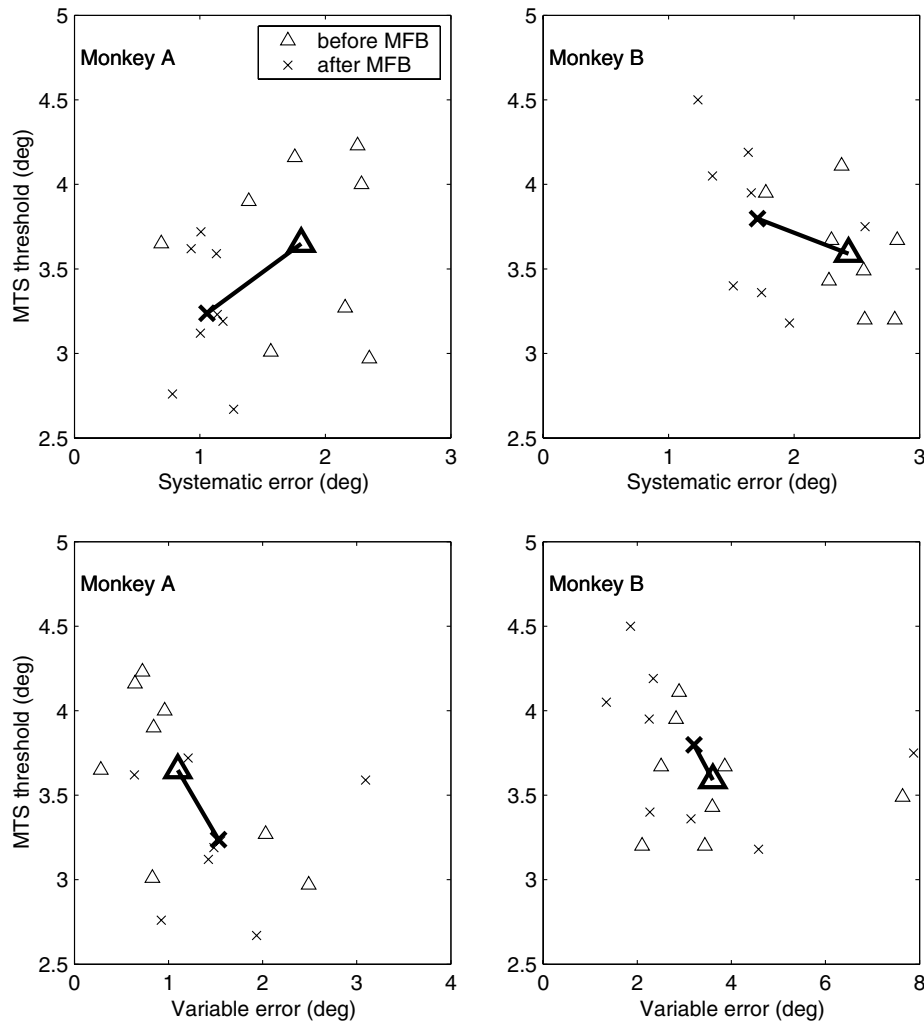


Fig. 8. MTS thresholds compared to systematic and variable saccade errors. Top row shows systematic errors and MTS thresholds before (triangles) and after (x's) feedback training. Each individual data points represent a different target direction. Bottom row shows variable errors and thresholds before (triangles) and after (x's) feedback training. Note that in the bottom row the x-axis scale is different for the two monkeys.

1994). Saccade accuracy for visual targets of certain eccentricity gets worse over time in the absence of a visual feed-back. This is indeed counterintuitive because normally, one would expect that “training” would improve accuracy. Both the accuracy improvement and error accumulation were faster for larger eccentricities than for smaller ones. For eccentricities smaller than 5 deg, in humans, Bahcall and Kowler (2000) reported a reduced adaptive effect as the post-saccadic time delay increases. Shafer et al. (2000) have shown, that in monkeys, the optimal adaptation effect occurs for a 80–200 ms delay of the post-saccadic feedback.

In addition to the accuracy improvement, we have also found that the change in the systematic errors is reversible. Thus, we have shown in Fig. 4 that visual feedback changes the magnitude of systematic errors in a reversible way. For both monkeys, performance in the MGS task, yields an increased saccade error, while in the MFB task saccade error has decreased. The inclu-

sion and removal of a post-saccadic visual cue, changes the context of the experiment. Thus, context dependent adaptation (Deubel, 1995) can be mediated by a gain change (Wallman & Fuchs, 1998). This may imply that the cerebellum connections to the saccadic pathway control the reversibility, becoming more active when the post-saccadic feedback is present and less active when the feedback cue is missing (Deubel, 1995; Scudder, Batourina, & Tunder, 1998). The systematic errors were accompanied by variable errors of saccade endpoints, shown in Fig. 5. The fact that there is no change in saccade spread over time may indicate that there is no memory component carried by the saccade variable errors. This is also supported by the results on the MTS tasks.

Another important finding was that the accuracy of spatial memory is not the source of the systematic errors. The results (Fig. 6) show no significant difference in separation thresholds before and after training, there-

fore excluding the hypothesized memory component. On the other hand, the motor component presence can be proved by significant difference in the systematic errors. Based on the experimental evidence, we conclude that the systematic errors are not due to the memory storage or read out, but they have a motor origin.

The inaccuracy of remembered saccades may reflect a targeting error process in the motor execution and not the retinotopic memory of the target locations (Gnadt et al., 1991; Stanford & Sparks, 1994). The non-retinotopic errors proposed by Gnadt et al. (1991) seem to occur in the oculomotor system downstream from SC, perhaps through interactions with cerebellum (Deubel, 1995), and are not reflected in the movement commanded by the SC.

The reduction of error magnitude for MGS when feedback is provided may be related to classical saccade adaptation (Deubel, 1995; Fuchs, Reiner, & Pong, 1996; Wallman & Fuchs, 1998). The “locus” of plasticity in saccade adaptation seems to be limited to cerebellum (Deubel, 1995; Scudder et al., 1998), since there is no neural correlate of adaptation in SC (Frens & Van Opstal, 1997), and the neurons in the brainstem saccadic burst generator are not “place” coded (Fuchs, Kaneko, & Scudder, 1985). The cerebellum plays an important role in various adaptive mechanisms (Deubel, 1995; Straube, Fuchs, Usher, & Robinson, 1997; Watanabe, Noto, & Fuchs, 2000), including both intra-saccadic and post-saccadic adaptation. In a neural model of saccadic adaptation Gancarz and Grossberg (1999) showed different types of saccadic gain adaptation depending on the task. The findings of Takagi, Zee, and Tamargo (1998) suggest that the cerebellar vermis is involved in every aspect of on-line control of saccades and also in the acquisition of adaptive ocular motor behavior. Thus, by introducing a post-saccadic visual cue, the saccadic system provides a fine calibration, through a motor adaptation process, driven by a visual error (Wallman & Fuchs, 1998). The mechanism of saccadic adaptation may differ among monkeys and humans, and may also depend on the timing and eccentricity of the adaptive visual feedback. In our experiments we were mainly concerned with the post-saccadic adaptation effects that were relevant for improved saccade accuracy. However, if MGS calibration and saccade adaptation shared a common mechanism, then the idea that saccade adaptation depends on cerebellar calibration of motor output would be consistent with the idea that MGS accuracy is controlled downstream from the site of memory storage.

In conclusion, our results show that the visual feedback provided after the completion of a saccadic eye movement, has a pronounced effect on the accuracy of oculomotor performance. (1) The change in systematic errors is not reflected in the variable errors. (2) The change in systematic errors is reversible. The increase and decrease in saccade error are mainly depending

upon the eccentricity of saccade. (3) These changes in saccade metrics may be part of an adaptation mechanism that adjusts the saccadic gain following alterations in the efficacy of the saccade generator. (4) The systematic errors are of a motor origin, and may be introduced by the motor structures downstream from the memory storage.

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